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Diversity of thalloid liverworts in Brazilian Savanna of Parque Nacional da Chapada das Mesas, Maranhão, Brazil

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Abstract

We investigate the diversity of thalloid liverworts in Parque Nacional da Chapada das Mesas (PNCM). Illustrations, descriptions, taxonomic characters, and notes on the geographic distributions of species, as well as an identification key, are provided. We collected specimens during the rainy seasons between 2017 and 2020. Six families, six genera, and seven species were recorded, of which five species are recorded for the first time from Maranhão state, two species are recorded for the first time from the Brazilian Northeast Region, and two are newly recorded from the Brazilian Cerrado. Our results increase in the number of thallose liverwort species in Maranhão by 57%. Our data add to what is known about PNCM, Maranhão, and Brazilian Cerrado liverworts, and reinforce the importance of PNCM for conservation.

Keywords

Cerrado, hotspot, Marchantiophyta, riparian forest, taxonomy

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Introduction

Liverworts or hepatics are nonvascular terrestrial plants with dominant, leafy or thalloid gametophytes and growing in humid places worldwide. They represent the oldest lineage of embryophytes (Gradstein et al. 2001; Qiu et al. 2006). However, Puttick et al. (2018) found support for Setaphyta, a moss–liverwort clade which is the sister group to all other bryophytes. There are about 7,500 species of liverwort distributed in 398 genera and 92 families (Söderström et al. 2016), and including 850 species of thalloid liverworts (11%), 500 simple thalloids (6%) (Jungermanniopsida), and 350 complex thalloids (5%) (Marchantiopsida) (Goffinet and Shaw 2009). In Brazil, 105 species of thalloid liverworts are recorded (Flora do Brasil 2020). Notable work on this group has been especially conducted in the southern and southeastern Brazil and include Hell (1969), Vianna (1985), Costa and Yano (1987), Costa (2008), and Ayub et al. (2014). Vianna (1985) focused mostly on Rio Grande do Sul and left a

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vast legacy of information about the genus *Riccia* L., ranging from notes about morphological characteristics of different species (Vianna 1990, 1992a, 1992b, 1994a, 1994b) to floristic surveys (1970, 1976, 1981, 1985).

Thalloid liverworts possess a dorsiventrally flattened gametophyte, lacking leaves and having a variable internal structure, and a thallus that can be dichotomous (e.g. *Riccia*) or pinnate. They are usually terrestrial, and being drought-tolerant plants, they can colonize arid environments, such as the Caatinga and Brazilian Cerrado (Gradstein and Costa 2003; Bischler-Causse et al. 2005). Myers et al. (2000) designated biodiversity hotspots having a high degree of endemism and highly threatened biodiversity. Brazil includes two hotspots: the Atlantic Forest and the Brazilian Cerrado, which are the most threatened of the Brazilian biomes.

The Brazilian Cerrado has been annually suffering great losses due to diverse anthropic activities, such as agricultural expansion, deforestation, industrial activity, and unchecked urban growth, but the destruction of the Brazilian Cerrado has mainly occurred due to the expansion of soy cultivation. The high biodiversity of the Cerrado is still only partly known to science and under great risk of extinction. The climate of this biome is Tropical Seasonal, with a wet and dry season; the annual average temperature is about 25 °C, and the average annual precipitation is 1,200–1,800. Sporadic, spontaneous fires also occur in this biome (Myers et al. 2000; Silva and Bates 2002; Klink and Machado 2005; Malhado et al. 2010; Latrubesse et al. 2019; Colli et al. 2020).

In the Brazilian Cerrado, 156 species of hepatics have been recorded. About 30 species of thalloid liverworts are recorded for this biome, and they are distributed in 11 families and 12 genera (Flora do Brasil 2020), corresponding to 27% of all thalloid liverworts species occurring in Brazil. Thus, the Brazilian Cerrado the second most species-rich biome for thalloid liverworts, and second only to the Atlantic Forest, which harbors 89% of the species. Despite being a large region with unique vegetation and climate, the Brazilian Cerrado has only one endemic thalloid liverwort, *Riccia sanguineisporis* Jovet-Ast, which occurs only in Mato Grosso (Gradstein and Costa 2003; Bischler-Causse et al. 2005).

There are currently 65 national parks in Brazil, and 15 national parks (or slightly less than 25% of the total national parks in Brazil) are within the Cerrado biome (Rocha et al. 2010). There are some studies on the bryophytes in national parks within this unique biome (e.g. Yano and Peralta et al. 2011; Pinheiro et al. 2012; Sousa and Câmara 2015; Carmo and Peralta 2016; Oliveira et al. 2018a), and the national parks in Minas Gerais are the best inventoried for this biome (Yano and Peralta et al. 2011; Sousa and Câmara 2015; Carmo and Peralta 2016).

Maranhão has two national parks: Parque Nacional dos Lençóis Maranhenses (dune and marine) and Parque Nacional da Chapada das Mesas (hereafter PNCM) (Brazilian Cerrado) (Rocha et al. 2010). Maranhão includes parts of the Amazonia, Caatinga, and Cerrado biomes, as well as transitional areas between them, giving the strate great importance to the ecology, biodiversity and conservation of species in Brazil (Rebêlo et al. 2003; Ab'Sáber 2003; Fiaschi and Pirani 2009).

PNCM has a great tourist interest due to its scenic beauty, including numerous sandstone plateaus and waterfalls. It includes one of the most conserved plateau areas of Maranhão, with typical Savanna phytophysionomies and numerous watercourses (ICMBIO 2020). To date, only one inventory of bryophytes has been undertaken in this park, which focused on mosses (Oliveira et al. 2018a). Contrary to its ecological richness, only 26 species of liverworts have been recorded in the state, with just six of them being thalloid liverworts (Silva et al. 2018; Flora do Brasil 2020). This low number of species is probably due to the scarcity of taxonomic studies in Maranhão on this group. Yano (2009) recorded three species of thalloid liverworts: *Cronisia weddellii* (Mont.) Grolle and *Riccia vitalii* Jovet-Ast in the municipality of Montes Altos, and *Riccia stenophylla* Spruce in the municipality of Loreto. Varão et al. (2011) recorded only one species (*R. stenophylla*) in the municipality of Governador Edson Lobão, and Oliveira et al. (2018b) recorded five species in the municipality of Caxias. All these species belong to the family Ricciaceae. The only taxonomic study focusing on thalloid liverworts in Maranhão was by Silva et al. (2018), but it only included species of the genus *Riccia* (five species).

Therefore, the purpose of our study is to inventory the species of thalloid liverworts in PNCM. We provide an identification key to species, as well as descriptions and comments on the species found. Our study will support future ecological work, conservation, and management within PNCM, which is highly important for the protection of the Brazilian Cerrado, a world hotspot (Myers et al. 2000).

Methods

PNCM was created on 12 December 2005 by presidential decree to preserve the Savanna areas threatened by the expansion of the agricultural and steel industry in southern Maranhão (Fig. 1). The park's extent is about 160,000 ha and lies within the municipalities of Carolina, Estreito, and Riachão in the middle Tocantins river basin. The area is a transition zone between the Brazilian Cerrado and Amazonia biomes and is at 97–681 m above sea level (MMA 2007; Martins et al. 2017).

PNCM has many watercourses, over 400 springs, and two large waterfalls: São Romão and Prata (IBGE 2019; ICMBIO 2020). Its vegetation cover is typical of the Brazilian Cerrado, with formations of gallery forest, riparian forest, cerradões (a forest formation with xeromorphic elements, and characterized by the mixed composition of species common to Cerrado, Gallery Forest, and mata seca), campo sujo (a herbaceous-shrubby physiognomy with spaced shrubs and sub-shrubs), and campo limpo (a herbaceous phytophysiognomy, with

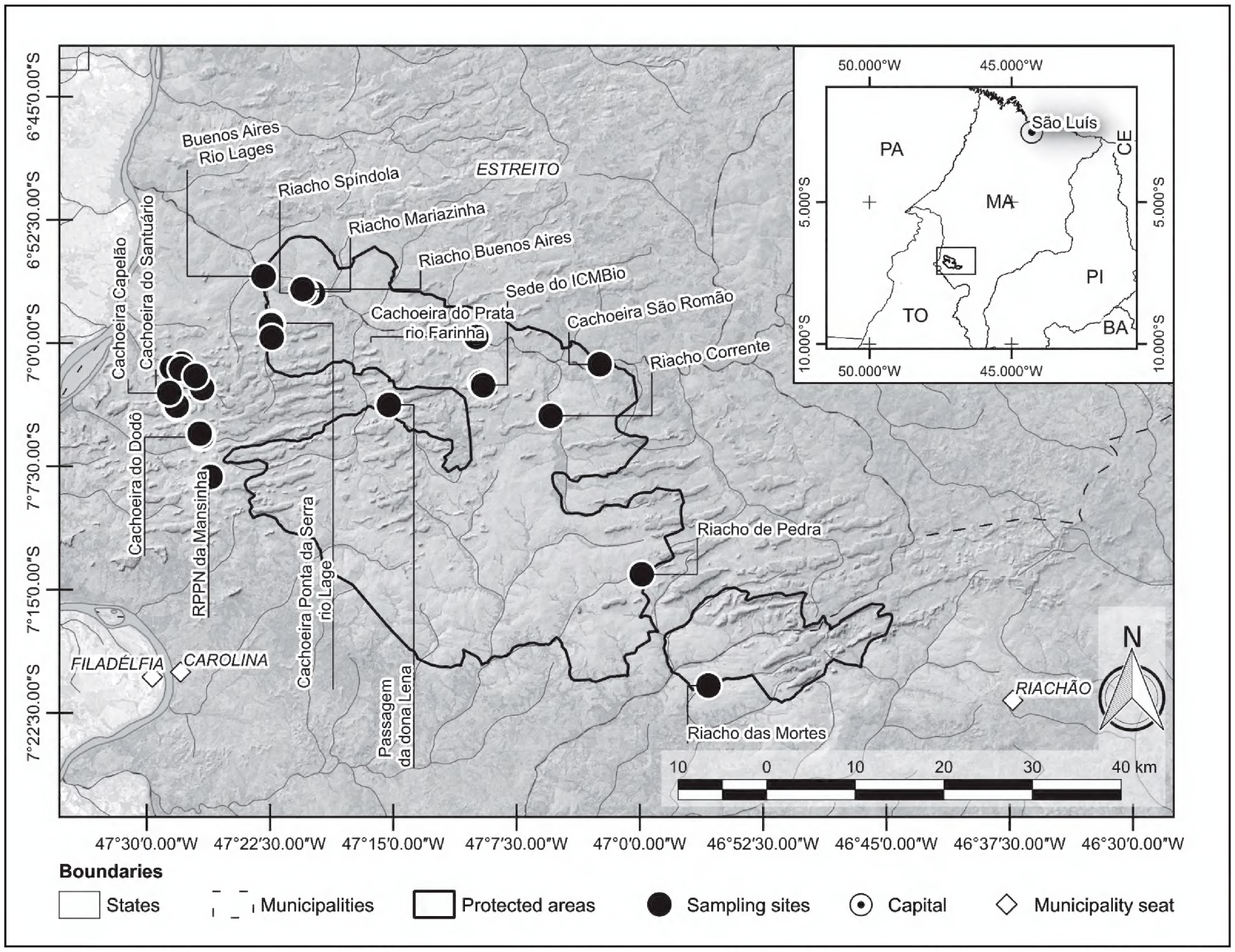


Figure 1. Map of the study area showing sampling sites inside and outside Parque Nacional da Chapada das Mesas, state of Maranhão, Brazil.

few shrubs and no trees) (Veloso et al. 1991). The region comprises plateaus, mountain ranges, and table mountains (mesas) (Veloso et al. 1991). The soils are formed by quartzarenic neosoils (SNUC 2020). The climate is tropical humid, with high temperatures throughout the year. The average annual temperature is about 26 °C, with low temperatures ranging from 25.2 °C in January to 27.8 °C in September, and a maximum temperature of about 36 °C in July and August (MMA 2007). There are two well-defined seasons: a dry summer and rainy winter (MMA 2007).

We collected specimens during four collecting expeditions in March and October 2017, June 2018, and February 2020 and included both rainy and dry seasons. Specimens were collected from waterfalls, along stream banks, and in gallery and riparian forests. We followed the methodology proposed by Yano (1989). Collecting efforts were carried out in several localities in PNCM, as well as in surrounding areas (Fig. 1). The specimens were dried and deposited in the CCAA herbarium. Duplicates of some species were sent to the RB herbarium.

The classification follows Crandall-Stotler et al. (2009). Our list of species in PNCM is in alphabetical order by family, genus, and species. We identified the specimens using the following literature: Uribe and Aguirre (1995), Gradstein and Costa (2003), and Bischler-Causse et al. (2005). The geographic distribution of the species is based on Bischler-Causse et al. (2005), Gradstein et al. (2001), Gradstein and Costa (2003), Flora do Brasil (2020), GBIF.org (2020), speciesLink (2020). and Tropicos.org (2020). Substrate type and the terms used in the species descriptions follow Gradstein et al. (2001).

Results

The species collected by us in PNCM represent 24% of the Brazilian Cerrado thalloid liverwort diversity. In our study area, we found seven species of thalloid liverworts, which are distributed in six genera and six families. These seven species represent 16% of the thalloid liverwort species in northeastern Brazil, a 57% increase in the number of thallose species known from Maranhão state (Silva et al. 2018; Flora do Brasil 2020). Most of the species found in our study are Neotropical in distribution, but *Cyathodium cavernarum* Kunze has a pantropical distribution (Gradstein and Costa 2003; Bischler-Causse et al. 2005; Söderström et al. 2020).

Key to the thalloid liverworts in PNCM

1 Thallus margin with sausage-shaped papillae. Sporophyte arising from leafy branches ..... ***Pteropsiella metzgeriiformis***

1′ Thallus margin without papillae. Sporophyte not arising from leafy branches..... **2**

2 Thallus a ventral structurally complex, divided into a photosynthetic dorsal layer and non-photosynthetic layer. Archegonium protected by involucre or embedded in the thallus. **3**

2′ Thallus structurally simple, not divided into layers, except in the central midrib. Archegonium protected by scale-like structures..... ***Symphyogyna leptothelia***

3 Dorsal surface of the thallus with pores..... 4

3′ Dorsal surface of the thallus without pores 5

4 Thallus more than 3 cells thick. Rhizoids with papillose walls. Ventral scales large (0.8 mm). Sporophyte on the dorsal surface of the thallus ..... ***Cronisia weddellii***

4′ Thallus very thin, only 2 or 3 cells thick. Rhizoids with smooth walls. Ventral scales absent (or present at the apex of the thallus and very small). Sporophyte on the ventral surface of the thallus . ..... ***Cyathodium cavernarum***

5 Thallus surface with whitish or blackish punctuations, margins crisped-undulate. Sporophyte arising from the thallus, and with linear capsule and thick seta ..... ***Monoclea gottschei***

5′ Thallus surface without whitish or blackish punctuations, margins flat. Sporophyte embedded in the thallus, and with a rounded capsule and no seta **6**

6 Thallus >1 mm wide, with violet scales extend beyond the margin ..... ***Riccia vitalii***

6′ Thallus <1 mm wide, without violet scales extend beyond the margin ..... ***Riccia stenophylla***

Corsiniaceae

***Cronisia* Berk.**

The genus is represented by two species in the Neotropics (Bischler-Causse 2005), and both are known to occur in Brazil and the Brazilian Northeast Region. The genus occurs in the Central-West, Northeast, North and Southeast regions in the Caatinga, Brazilian Cerrado, Atlantic Forest, and Pantanal biomes. Only *Cronisia weddellii* (Mont.) Grolle occurs in Maranhão state (Flora do Brasil 2020).

***Cronisia weddellii* (Mont.) Grolle**

Figure 2A–E

Material examined. BRAZIL – Maranhão • Carolina, Parque Nacional Chapada das Mesas, Rio Farinha; 06° 56′43″S, 047°20′31″W; alt. 179 m; 11 Mar. 2017; J.A.S Silva 020 col.; CCAA 1502. • ibid.; J.A.S Silva 021 col.; CCAA 1553. • ibid.; Cachoeira do Prata; 06°59′41″S, 047° 09′53″W; alt. 197 m; 06 Jun. 2018; J.A.S Silva 218 col.; CCAA 1532. • ibid.; J.A.S Silva 222 col.; CCAA 1521. • ibid.; J.A.S Silva 223 col.; CCAA 1539. • ibid.; J.A.S Silva 227 col.; CCAA 1513. • ibid.; Cachoeira São Romão 07°04′25″S, 047°05′26″W; 7 Jun. 2018, J.A.S Silva 253 col.; CCAA 1517. • ibid.; Riacho Buenos Aires; 06°56′43″S, 047°20′31″W; alt. 179 m; 08 Jun. 2018; J.A.S Silva 300 col.; CCAA 1589. • ibid.; J.A.S Silva 302 col.; CCAA 1505.

Identification. Plants terrestrial and rupicolous. Thallus dichotomous, light green, whitish, or violet, 0.9–0.20 × 0.8–1.1 mm, without central midrib; main axis wider; dorsal surface chlorophyllose; epidermal pores with 5 or 6 ring cells; thallus in cross-section with one layer of air chambers with chlorophyllose filaments; ventral surface whitish; margin entire, green hyaline; ventral scales violet, large (0.8 mm long), with a filiform appendage, not extending beyond the margin. Sporophyte on the dorsal surface; involucre covering the sporophyte; capsule spherical; spores spherical, brown to dark brown; elaters short, no more than twice as wide.

Cronisia weddellii can be confused with species of *Riccia*. However, *C. weddellii* differs by having the cavities in the thallus containing antheridia, pores with ring cells, appendage scales filiform and sporophyte covered by the involucre (Bischler-Causse et al. 2005). Two species have been recorded from northeastern Brazil, *C. weddellii* and *C. fimbriata* (Nees) Whittem., of which the latter occurs mainly in the Caatinga (Yano and Porto 2006; Yano et al. 2009; Germano et al. 2016). *Cronisia weddellii* differs from *C. fimbriata* by having non-raised epidermal pores and scales that do not extend beyond the margins of the thallus.

Distribution and ecology. Neotropical (Bischler-Causse et al. 2005). In Brazil, it is known from Caatinga (Alagoas, Bahia, Ceará, Paraíba, Piauí and Pernambuco), Atlantic Forest (Espírito Santo), and Savanna biomes (Goiás, Maranhão, Mato Grosso, and Tocantins) (Gradstein and Costa 2003; Yano 2009; Flora do Brasil 2020). It is a typical species of the Brazilian Cerrado and Caatinga and tolerant to drought and high temperatures. We collected this species on soil and rocks on riverbanks where it was growing with mosses of the family Bartramiaceae. We observed that young plants differ from adults in the color of the thallus and shape of the scales. The thallus in young is light green, with scales almost or entirely hyaline and with only the apex violet; in adults the thallus is whitish to violet.

Cyathodiaceae

***Cyathodium* Kuntze**

The genus is represented by five species in the Neotropics (Bischler-Causse 2005). Only *Cyathodium cavernarum* has been recorded for Brazil, where it occurs in the Central-West, Northeast, and Southeast regions and in the following biomes: Brazilian Cerrado, Atlantic Forest and Pantanal (Flora do Brasil 2020). Our records of this species from PNCM are the first from Maranhão state.

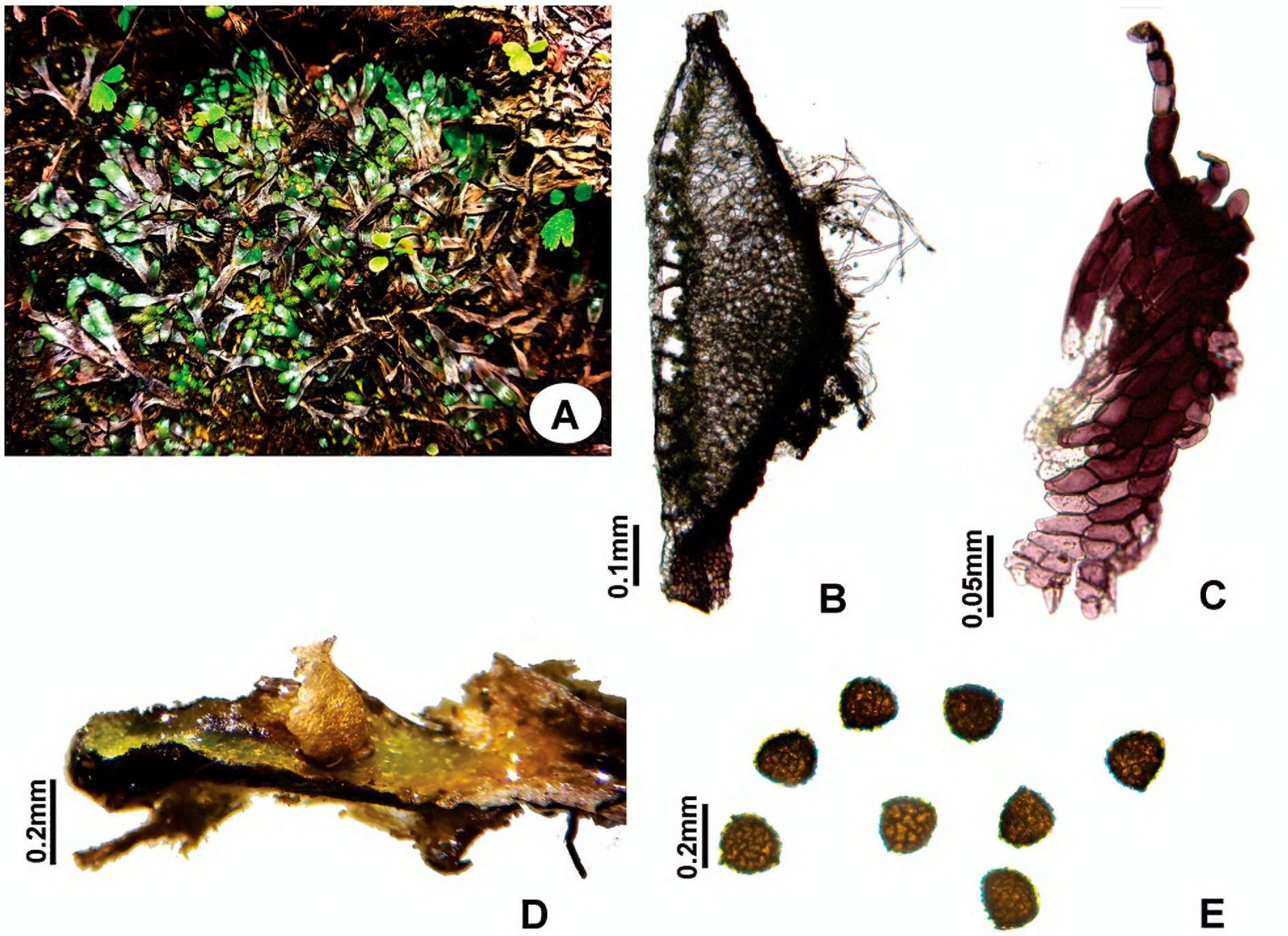


Figure 2. *Cronisia weddellii* (J.A.S.Silva 222 CCAA). **A.** Habit. **B.** Cross-section of thallus. **C.** Scale. **D.** Thallus with female involucre. **E.** Spores. Photos: J.A.S. Silva.

Cyathodium cavernarum Kunze

Figure 3A–E

Material examined. BRAZIL – Maranhão • Carolina, Parque Nacional Chapada das Mesas, Cachoeira São Romão; 07°04′25″S, 047°05′26″W; alt. 256 m; 07 Jun. 2018; J.A.S Silva 275 col.; CCAA 1587. • ibid., Complexo Pedra Caída, cachoeira do Santuário; 07°02′44″S, 047°27′01″W; alt. 128 m; 07 Feb. 2020; J.A.S Silva 551 col.; CCAA 2696.

Identification. Plants rupicolous. Thallus obcuneate, very thin, only 2 or 3 cells wide, with smooth rhizoids, bright green to yellowish, 4–6 × 0.6–1.0 mm, without central midrib; main axis broad and flat; dorsal surface of chlorophyllose thallus with epidermal pores with a ring of 6–8 cells; thallus in cross section with one layer of air chambers without chlorophyllose filaments; ventral surface with chlorophyllose cells; margin entire, greenish; ventral scales reduced or absent. Sporophyte on the ventral surface of the thallus (near the apex); involucre sac-shaped; capsule ovoid, dark brown, opening with an operculum; spores spherical and densely spinose, dark brown; elaters long.

Cyathodium cavernarum differs from other species of thallose liverworts in the study area by having a bright green thallus with few layers of cells, and a sporophyte capsule opening through a ring of cells. It differs from other species of *Cyathodium* by having the rhizoids with smooth walls, a sporophyte with an operculum, and spiny spores (Bischler-Causse et al. 2005).

Distribution and ecology. Worldwide (Bischler-Causse et al. 2005 and Söderström et al. 2020). Atlantic Forest (Minas Gerais), Caatinga (Bahia, Ceará, Paraíba, Pernambuco, and Piauí), Brazilian Cerrado (Goiás, Mato Grosso, Maranhão, and São Paulo), Pantanal (Mato Grosso do Sul) (Söderström et al. 2020; Flora do Brasil 2020; new data). We collected *C. cavernarum* on shaded rocks with a thin trickle of water running over the gametophyte. It was collected fertile only at the end of the rainy season.

Lepidoziaceae

Pteropsiella Spruce

This genus is represented by two species in the Neotropics, *P. frondiformis* Spruce and *P. metzgeriiformis* Spruce ex Steph. (Söderström et al. 2016; Flora do Brasil 2020). These species are distributed mainly in the North and Southeast regions of the country, in the Amazonia and Atlantic Forest biomes (Flora do Brasil 2020). Our record of *P. metzgeriiformis* is the first from the Brazilian Cerrado, the Northeast Region, and Maranhão.

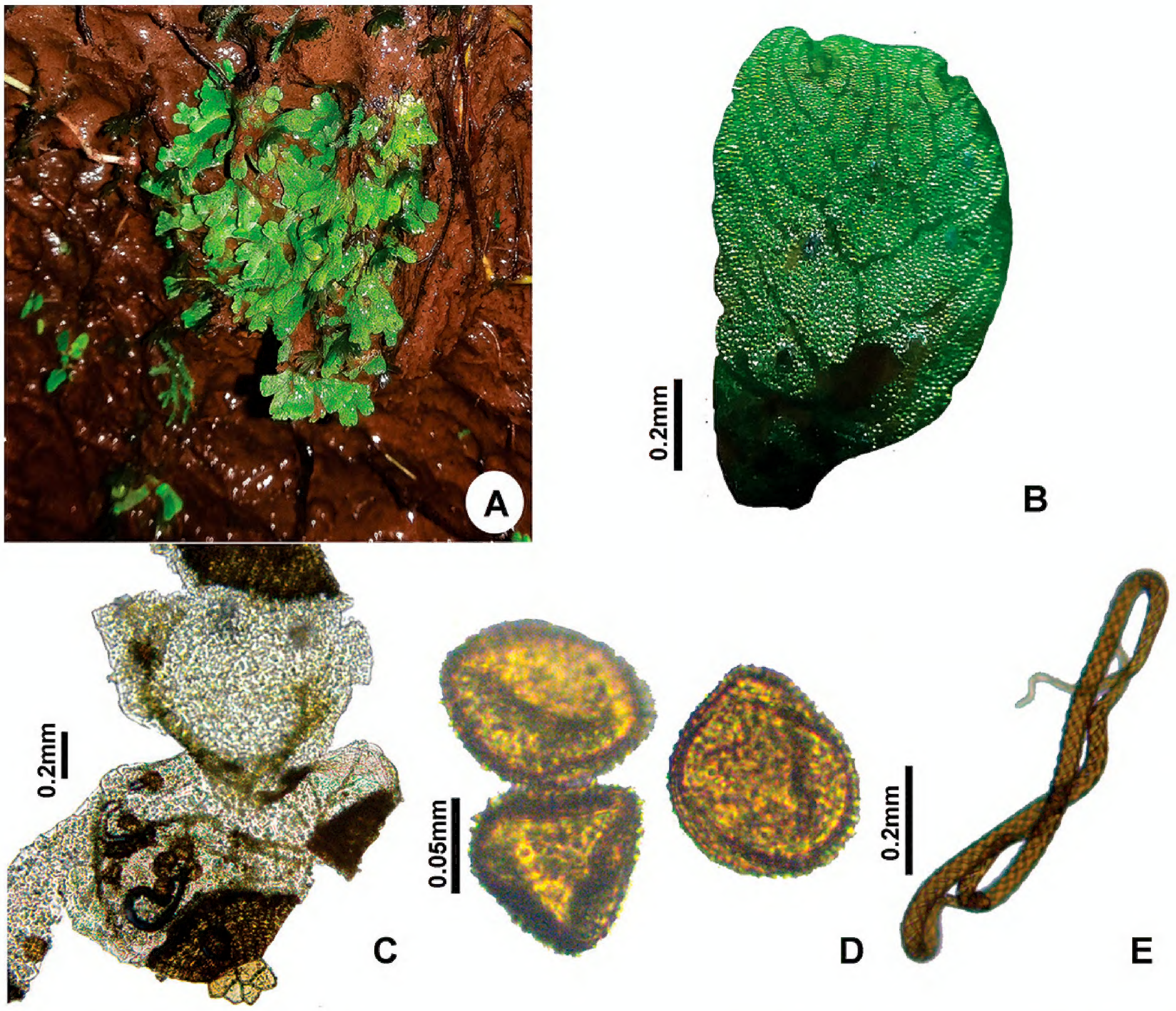


Figure 3. *Cyathodium cavernarum* (J.A.S.Silva 275 CCAA). **A.** Habit. **B.** Thallus. **C.** Capsule open with annulus cells at apex. **D.** Spores. E: Elaters. Photos: J.A.S.Silva.

***Pteropsiella metzgeriiformis* Spruce ex Steph.**
Figure 4A–D

Material examined. BRAZIL – Maranhão • Carolina, Parque Nacional Chapada das Mesas, Riacho Corrente; 07° 04′25″S, 047°05′26″W; alt. 277 m; 07 Jun. 2018; J.A.S Silva 294 col.; CCAA 1558.

Identification. Plants terrestrial. Thallus light green, 10–30 × 0.3–0.5 mm; branches inserted ventrally; midrib rounded in cross-section, with six cortical cells (two dorsal and four ventral, and less than 15 medullary cells); wings narrow and unistratose; dorsal surface of thallus without pores and air chambers; ventral surface with chlorophyllose cells; margin toothed, green, with one or two sausage-shaped papillae; scales absent. Sporophyte arising from leafy branches.

Pteropsiella is sometimes misidentified as species of Metzgeriaceae because they also have a unistratose, flat thallus, with a midrib. However, *Pteropsiella* has a toothed, green margin with one or two sausage-shaped papillae, and rhizoids present only on the midrib, while Metzgeriaceae has thallus margins with rhizoids and gametoecia on the ventral side of the midrib. *Pteropsiella metzgeriiformis* differs from *P. frondiformis* by the light green thallus with fewer than 15 medullary cells, while *P. frondiformis* has a dark green thallus with more than 15 medullary cells.

Distribution and ecology. Brazil and Colombia (Lisboa 1976; Gradstein and Costa 2003; Pinzón et al. 2003; Carmo and Peralta 2016; Costa et al. 2017). Brazilian biomes and states: Amazonia (Amazonas and Roraima) and Atlantic Forest (Minas Gerais) (Carmo and Peralta 2016; Costa et al. 2017); and Brazilian Cerrado (Maranhão; new data). We collected this species near an open, sunny, sandy stream bank.

Monocleaceae

***Monoclea* Hook.**

This genus comprises two species, *Monoclea gottschei* Lindb. and *M. forsteri* Hook., of which the latter occurs in New Zealand (Gradstein and Costa 2003; Söderström et al. 2016). Until now, *M. gottschei* had been recorded in the North, Northeast, Ssoutheast, and South regions of Brazil, in the Amazonia, Atlantic Forest, and Pampas

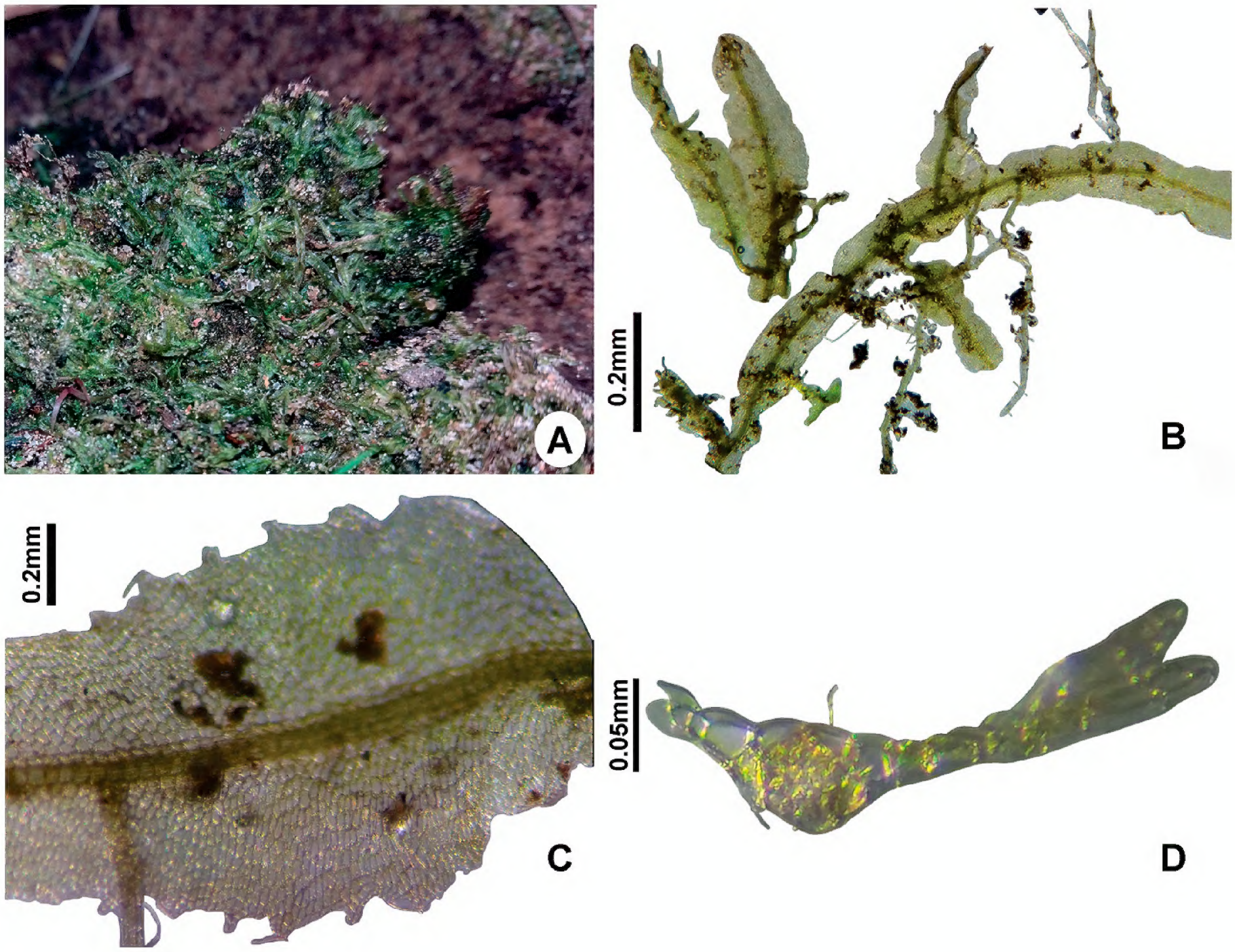


Figure 4. *Pteropsiella metzgeriiformis* (J.A.S.Silva 294 CCAA). **A.** Habit. **B.** Thalli, ventral view. **C.** Margin of thallus toothed with papillae. **D.** Cross section of thallus. Photos: J.A.S.Silva.

biomes (Flora do Brasil 2020). Our new records are the first of the genus from the Brazilian Cerrado biome and Maranhão state.

***Monoclea gottschei* Lindb.**

Figure 5A–D

Material examined. BRAZIL Maranhão • Carolina, Complexo Pedra Caída, cachoeira do Santuário; 07°02′ 44″S, 047°27′01″W; alt. 128 m; 07 Feb. 2020; J.A.S Silva 552 col.; CCAA 2578. • ibid., J.A.S Silva 557 col.; CCAA 2697.

Identification. Plants rupicolous. Thallus dark green, 20–30 × 5–10 mm wide, dichotomous, without central midrib, homogeneous; dorsal surface with chlorophyllose cells and without epidermal pores, densely spotted by whitish or darkish dots (observed in fresh material); air chambers absent; ventral surface with chlorophyllose cells; margins usually crispate-undulate. Sporophyte not seen.

Monoclea gottschei is a large plant, 2–3 cm long, with crispate-undulate margins. This species is sometimes misidentified as *Dumortiera hirsuta* (Sw.) Nees because it has a green, flattened thallus, without pores and air chambers, and often occurs in the same habitat. Otherwise, *M. gottschei* differs from *D. hirsuta* by having whitish dots on the thallus in fresh material and no ventral bundle of the rhizoid (Gradstein et al. 2001).

Distribution and ecology. Neotropical (Gradstein and Costa 2003; Gradstein 2017; Flora do Brasil 2020; GBIF.org 2020). Brazilian biomes and states: Amazonia (Amazonas), Atlantic Forest (Espírito Santo, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, and São Paulo), and Pampas (Rio Grande do Sul) (Gradstein and Costa 2003; Flora do Brasil 2020); and Cerrado (Maranhão; new data). We collected this species on shaded rocks near a waterfall.

Pallaviniaceae

***Symphyogyna* Nees & Mont.**

The genus is represented by 11 species in the Neotropics (Uribe and Aguirre 1995; Gradstein and Costa 2003; Flora do Brasil 2020). Five species are known to occur in Brazil, in the Central-West, Northeast, North, and Southeast regions, in the Atlantic Forest, Caatinga, Cerrado, and Pantanal biomes (Flora do Brasil 2020). Of these five species, three occur in the Northeast Region. We report the first records of *Symphyogyna leptothelia* for the Northeast Region, making it the fourth species of the genus recorded for this region, and the first time that the genus is reported from Maranhão state.

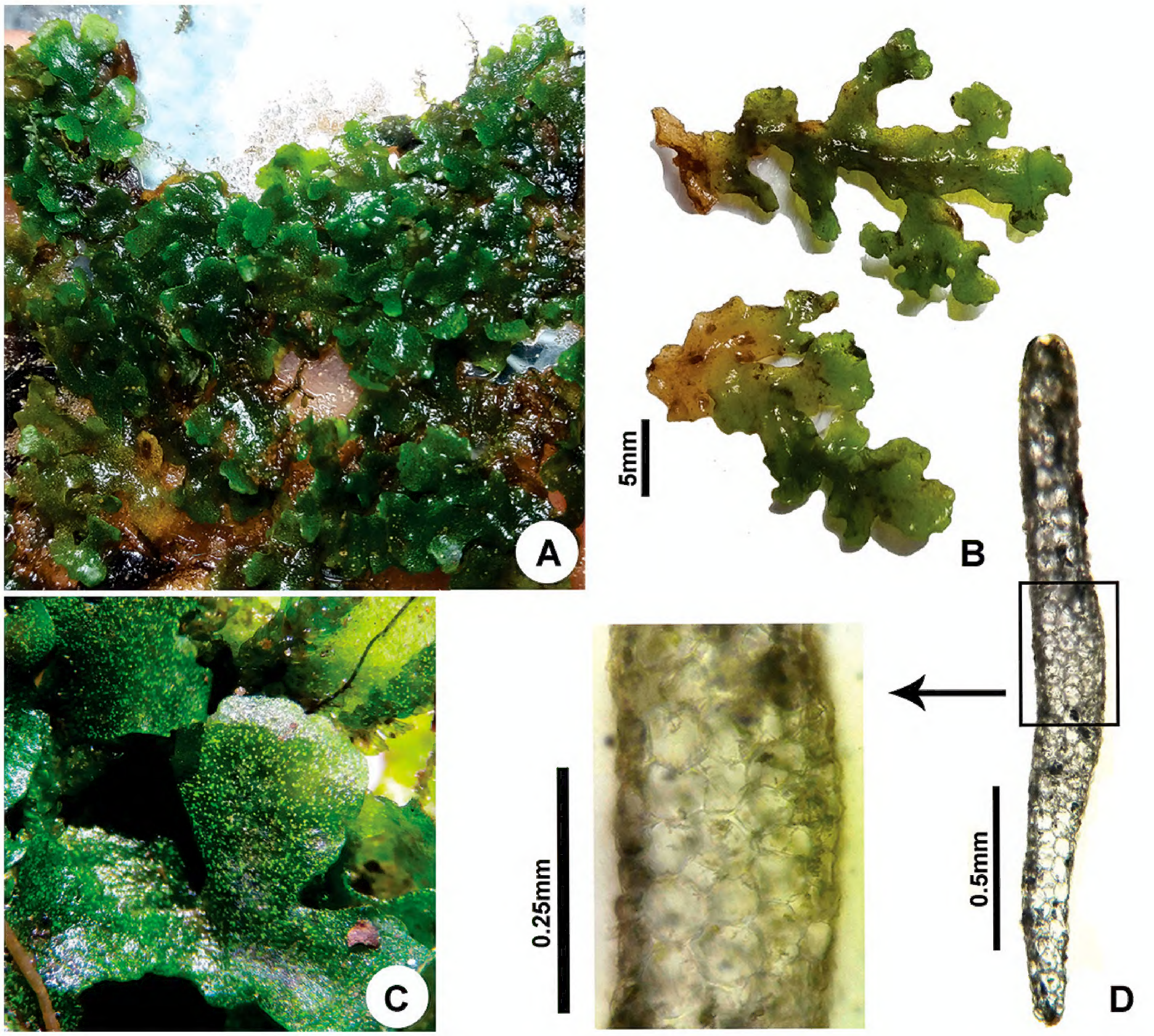


Figure 5. *Monoclea gottschei* (J.A.S.Silva 552 CCAA). **A.** Habit. **B.** Thalli. **C.** Thallus with whitish dots. **D.** Cross section of thallus. Photos: J.A.S.Silva.

***Symphyogyna leptothelia* Taylor**

Figure 6A–F

Material examined: BRAZIL – Maranhão • Carolina, Parque Nacional Chapada das Mesas, passagem da Dona Lena 07°03′45″S, 047°15′16″W; alt. 230 m; 07 Jun. 2018; J.A.S Silva 292 col.; CCAA 1528. • ibid.; 04 Feb. 2020; J.A.S Silva 491 col.; CCAA 2628.

Identification. Plants rupicolous. Thallus dichotomous, dark green, 21–26 × 2.2–5 cm, with central midrib; main axis convex to flat, 0.1 mm wide, with single prosenchyma band; wings large (0.2 mm); dorsal surface in cross-section without epidermal pores and air chambers; ventral surface with chlorophyllose cells; margin toothed; teeth with 5 or 6 cells; dorsal scales covering the archegonium. Sporophyte not seen.

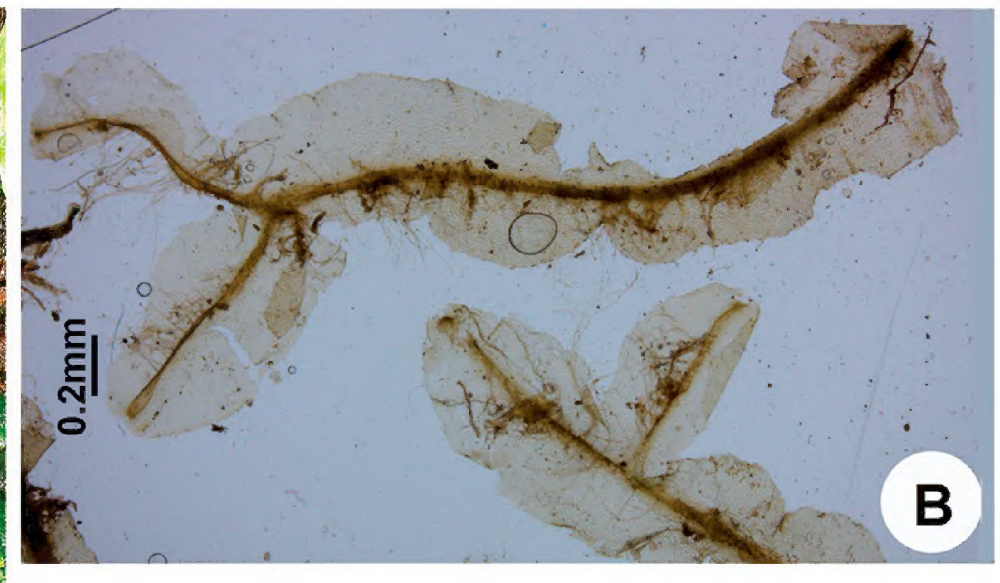
Symphyogyna leptothelia grows prostrate on soil, and the thallus has wide undulate wings, a prominent central midrib with a single strand of prosenchyma tissue, and a toothed margin. *Symphyogyna aspera* Steph. is sometimes confused with *S. leptothelia* due to the prostate habit, dark green thallus, and toothed margin. However, *S. leptothelia* has entire wings that are not divided into segments and a toothed thallus apex, while *S. aspera* has lobate wings, divided into segments, and a non-toothed thallus apex.

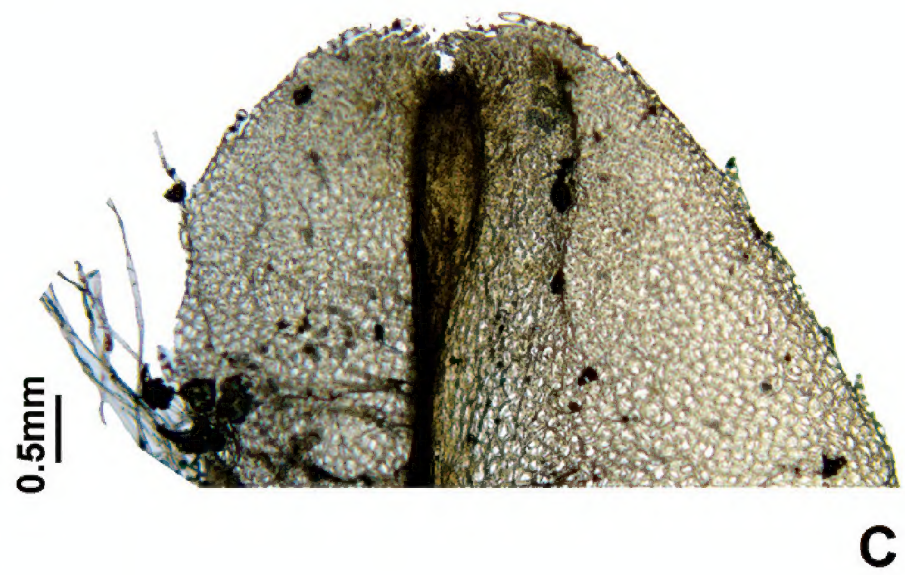
Distribution and ecology. Neotropical (Uribe and Aguirre 1995; Gradstein and Costa 2003; GBIF.org 2020; Tropicos.org 2020). Brazilian biomes and states: Atlantic Forest (Espírito Santo, São Paulo, and Paraná), Brazilian Cerrado (Goiás, Maranhão; new data), Mato Grosso do Sul, Minas Gerais) (Flora do Brasil 2020). We collected this species on shaded rocks near the sandbank of a stream in a riparian gallery forest.

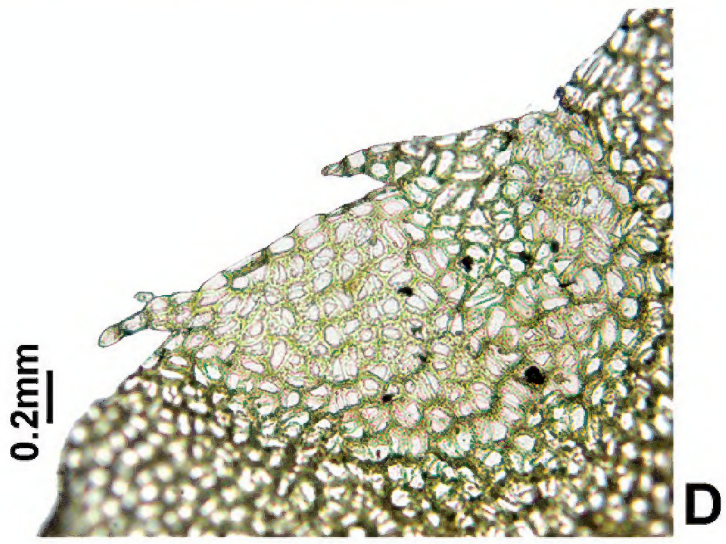
Ricciaceae

***Riccia* L.**

This genus comprises 53 species in tropical America, of which 36 are recorded from Brazil (Bischler-Causse et al. 2005; Costa and Peralta 2015). It occurs in all regions of Brazil, and occurs in the Amazonia, Atlantic Forest,







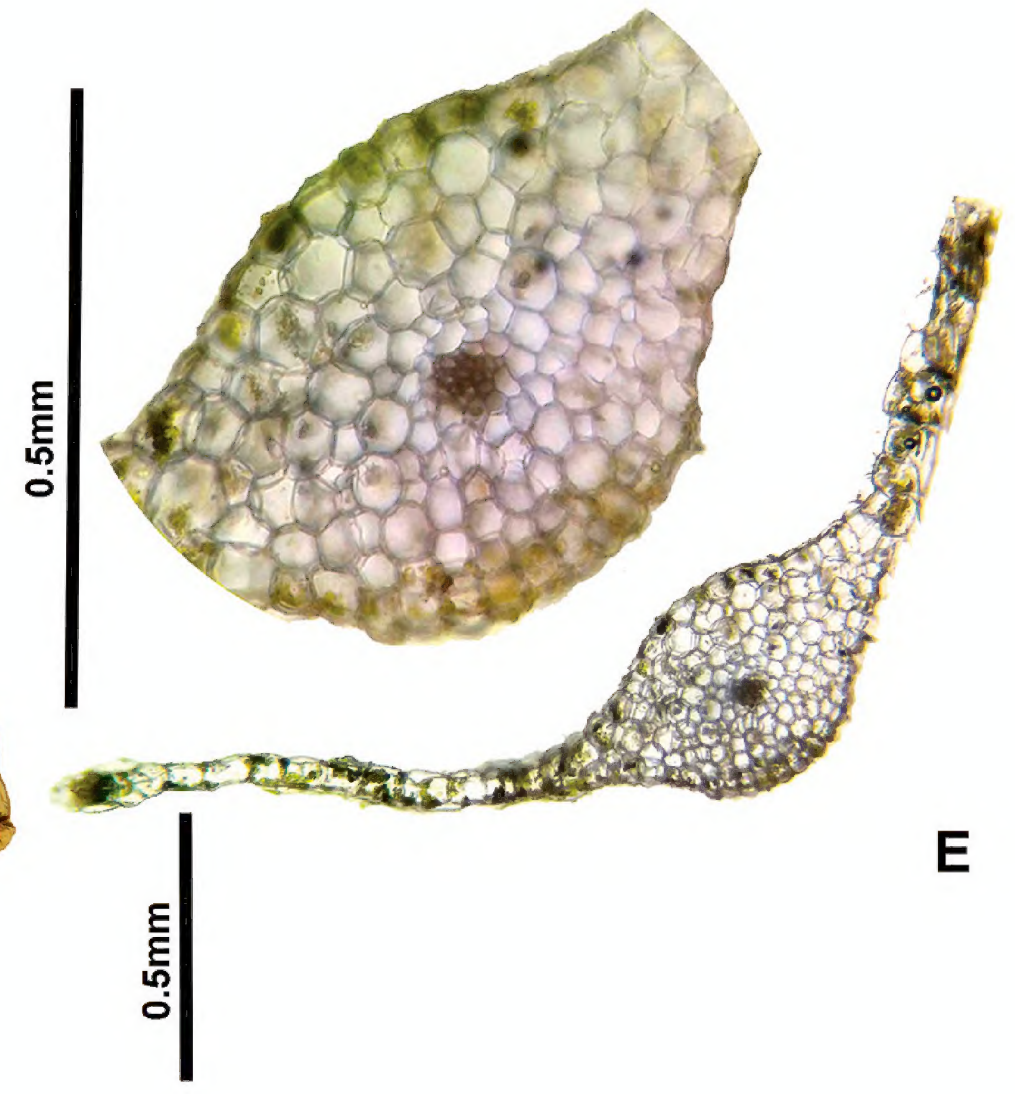


Figure 6. *Symphyogyna leptothelia* (J.A.S.Silva 292 CCAA). **A.** Habit. **B.** Thalli, ventral view. **C.** Apex of thallus. **D.** Detail of teeth of the margin. **E.** Cross section of thallus. **F.** Scale. Photos: J.A.S.Silva.

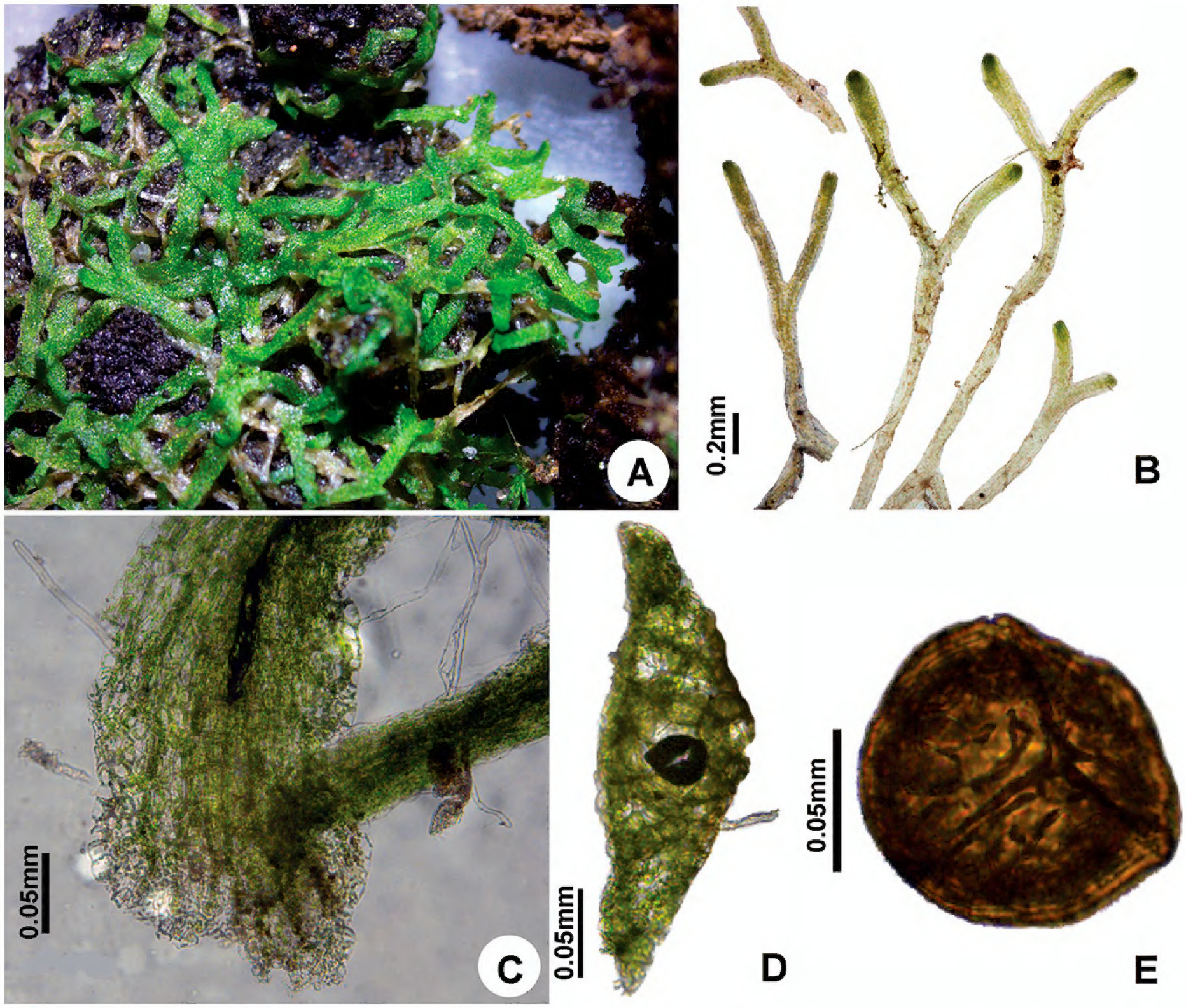


Figure 7. *Riccia stenophylla* (J.A.S.Silva 202 CCAA). **A.** Habit. **B.** Thalli. **C.** Apex of thallus. **D.** Cross section of thallus. **E.** Spore, distal face. Photos: J.A.S.Silva.

Caatinga, Pampas, Pantanal and Brazilian Cerrado biomes (Flora do Brasil 2020).

Riccia stenophylla **Spruce**

Figure 7A–E

Material examined. BRAZIL – Maranhão • Carolina, Parque Nacional Chapada das Mesas, Cachoeira do Prata; 06°59′41″S, 047°09′53″W; alt. 197 m; 29 Oct. 2017; J.A.S. Silva 146 col.; CCAA 1533. • ibid.; J.A.S. Silva 202 col.; CCAA 1578. • ibid.; J.A.S. Silva 229 col.; CCAA 1551.

Identification. Plants terrestrial or semiaquatic. Thallus bright green, dichotomous, 2–8 × 0.2–0.4 mm, linear, without central midrib; dorsal surface with or without a slight median groove with photosynthetic cells, with pores bounded by four or five cells; air chambers in one or two layers; ventral surface greenish; margin entire, green to hyaline; ventral scales hyaline, 0.01 mm long. Sporophytes immersed in the thallus, forming a bulge ventrally, without involucre; capsule spherical, brown; spores tetrahedral, brown to yellow, without elaters.

Riccia stenophylla is a terrestrial or semiaquatic plant, with a long and slender thallus, smooth median area with or without a groove, and sporophyte forming a bulge ventrally. *Riccia stenophylla* is sometimes misidentified as *R. fluitans* L. since these species are both semiaquatic and have a thin stem and internal sporophyte forming a ventral bulge in the thallus. However, *R. fluitans* has a Holarctic distribution (Gradstein and Costa 2003; Stotler and Crandall-Stotler 2017), while *R. stenophylla* is a Neotropical species (Gradstein et al. 2016).

Distribution and ecology. Tropical and subtropical America (Argentina, Brazil, Colombia, Costa Rica, United States, Guatemala, Mexico, Nicaragua, Panama, Paraguay, Peru, and Uruguay) (Bischler-Causse et al. 2005; Gradstein et al. 2016; GBIF.org 2020). Brazilian biomes and states: Atlantic Forest (Espírito Santo, Paraná, Rio de Janeiro, Santa Catarina, and São Paulo), Caatinga (Bahia, Ceará, Paraíba, and Pernambuco), Cerrado (Goiás, Maranhão, and Mato Grosso), Pantanal (Mato Grosso do Sul), and Pampas (Rio Grande do Sul) (Flora do Brasil 2020). We found this species only at the end of the rainy season in ravines near rivers and streams in open habitats which were partially exposed to the sun.

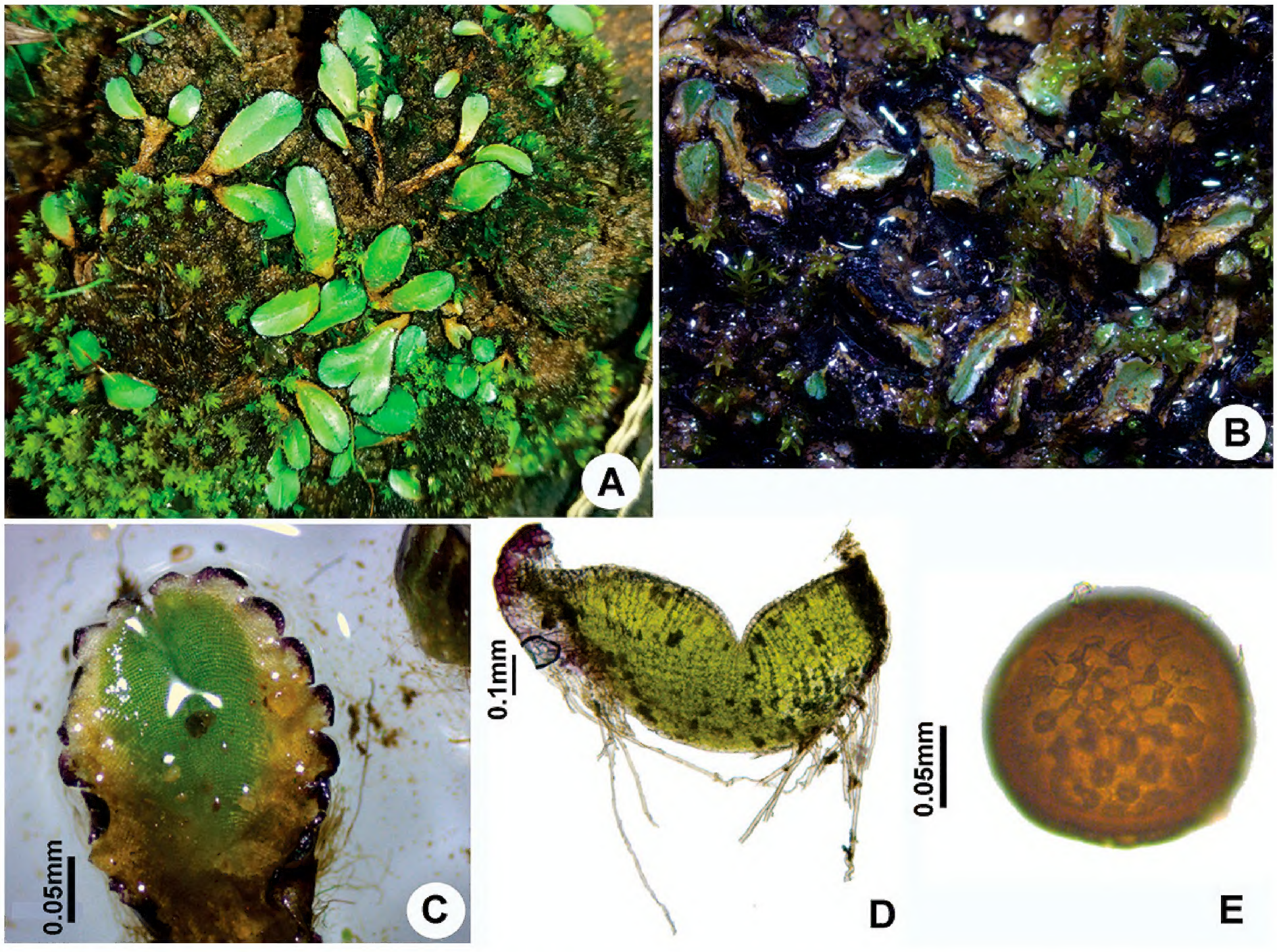


Figure 8. *Riccia vitalii* (J.A.S.Silva 073 CCAA). **A.** Habit (Wet). **B.** Herbarium specimen (habitat dry). **C.** Thallus in dorsal view with scales on the margin. **D.** Cross section of thallus. **E.** Spore, proximal face. Photos: J.A.S.Silva.

***Riccia vitalii* Jovet-Ast.**

Figure 8A–E

Material examined. BRAZIL – Maranhão • Carolina, Parque Nacional Chapada das Mesas, Cachoeira do Prata; 06°59′37″S, 047°09′57″W; alt. 197 m; 12. Mar. 2017; J.A.S. Silva 073, 075, 079 col.; CCAA 1564; 1494; 1507. • Estreito, Parque Nacional Chapada das Mesas, 06°59′39″S, 047°09′56″W; 12 Mar. 2017; J.A.S. Silva 085 col.; CCAA 1775.

Identification. Plants rupicolous. Thallus dichotomous, dark green, 5–8 × 2–4 mm, without central midrib; dorsal surface with one deep, median groove with photosynthetic cells; pores absent; ventral surface whitish to violet, without photosynthetic cells; margin green to hyaline; ventral scales large, 0.05 mm long, violet, without filiform appendages, and extending beyond the margin. Sporophytes immersed in the thallus, without involucre; capsule spherical, brown; spores subspherical to subtetrahedral, reddish to dark brown, without elaters.

Riccia vitalii is terrestrial and differs from *R. stenophylla* in having the thallus with a deep median groove and large violet scales extending beyond the margin. In Brazil, *R. vitalii* when sterile can be misidentified as *Riccia weinionis* Steph. because both have a thallus with a deep median groove and dorsal cells with vertical bands of longitudinal thickenings which are seen in the thallus cross-section). However, *R. vitalii* can be easily distinguished from *R. weinionis* by the form and ornamentation of the spores. In *R. vitalii*, the spores are subspherical to subtetrahedral, with a granular proximal face and an evident trilete mark, whereas in *R. weinionis* the spores are tetrahedral with a proximal face with few areolas and without a trilete mark (Silva et al. 2018).

Distribution and ecology. Neotropical (Costa Rica, Paraguay, Colombia, and Brazil) (Bischler-Causse et al. 2005; Gradstein et al. 2016). In Brazil, it occurs in the Amazonia (Amazonas), Atlantic Forest (Espírito Santo), Caatinga (Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte and Sergipe), Pampas (Rio Grande do Sul), Pantanal (Mato Grosso do Sul), and Cerrado (Goiás, Maranhão, and Tocantins) biomes (Flora do Brasil 2020). We found it growing in open, sunny habitats near waterfalls.

Discussion

The thalloid liverworts collected in PNCM belong to four orders: Jungermanniales, Marchantiales, Metzgeriales, and Pallaviciniales. The majority (five) of the species are in Marchantiales. In the Neotropics, this is the most species-rich order, with 103 species in 12 families and 13 genera (Bischler-Causse et al. 2005; Villarreal et al. 2015; Söderström et al. 2016).

Even though PNCM is located in the Brazilian Cerrado and has some transitional vegetation types, such as Cocais Forest, we found families more similar to the Caatinga biome than another study in the Cerrado biome by Gradstein and Costa (2003). In our study, the similarity with thalloid liverworts of the Caatinga biome is because we focused on gallery forest, but possibly also may have been influenced by the collection methods.

We present records of five species of thalloid liverworts newly reported from Maranhão state, and most notably *Pteropsiella metzgeriiformis* and *Monoclea gottschei*, which are also recorded for the first time from the Brazilian Cerrado. Until now, *P. metzgeriiformis* was only reported from Amazonia and the Atlantic Forest (Carmo and Peralta 2016; Lisbôa 1976). In Brazil, *M. gottschei* is distributed in the Amazonia, Atlantic Forest, Brazilian Cerrado, and Pampas biomes, occurring mainly in mountainous regions usually in habitats without drought stress and with high humidity throughout the year (Hell 1969; Costa and Yano 1987; Gradstein and Costa 2003; Flora do Brasil 2020).

Cyathodium and *Monoclea* were only collected in microhabitats near waterfalls where they were living on wet, shaded cliffs. The restricted occurrence of *Cyathodium* in extremely moist habitats, such as near waterfalls, might be because its thallus has few cell layers, and lacking a cell layer for water storage, it is impossible for this species to colonize drier habitats unlike *Riccia* and *Cronisia* (Bischler-Causse et al. 2005). *Cronisia weddellii* was the most abundant species that we collected and occurred at the majority of our sites. This species is frequently collected in northeastern Brazil (Yano 2009; Germano et al. 2016; Oliveira et al. 2018b; Silva et al. 2018).

The most species-rich family of thalloid liverworts in the Neotropics is Ricciaceae (Bischler-Causse et al. 2005). We expected to find more species of this family because there are two centers of diversity for this family in Brazil (Caatinga and Pampa; Ayub 2014; Reis 2015) and Maranhão has two (Amazon basin and the Palm Forest) of the six main zones where *Riccia* occurs in the country (Jovet-Ast 1991). In our study, the Ricciaceae had the most species (two), while each of the other families were represented by only one species.

Riccia was collected in places exposed to the sun, and this preference for sunny, exposed habitats can explain the wide distribution of this genus in the tropics. *Riccia* has physiological characteristics, such as spores and stems adapted to desiccation, that allow it to survive drought. Additionally, rapid development of gametophytes and spores when water is available may offer another explanation (Bischler-Causse et al. 2005).

Most of the species found in our study have a rupicolous habit, which is possibly due to the large number of rocks near the streams and waterfalls. However, the soil characteristics must be considered, as the soil is porous and susceptible to erosion, which hinders the accumulation of water on the surface. This may force plants to grow on rocky substrates where they are less disturbed by erosion of their substrate (Martins et al. 2017). However, even where living and dead trunks are abundant, such as gallery forests in the Brazilian Cerrado and Atlantic Forest biomes, thalloid liverwort species tend to grow on rocks or soil (Hell 1969; Costa 1988; Yano and Pôrto 2006; Yano and Peralta et al. 2011; Carmo and Peralta 2016). Another possible explanation for plants growing on rocky surfaces is that they posses ventral cells specialized in water absorption. However, ecological studies are necessary to confirm this. While *Riccia stenophylla* and *P. metzgeriiformis* are unique because of their terrestrial habit, they were always found near river banks and, in the case of *R. stenophylla*, sometimes submerged in water.

We collected most of the thalloid liverwort species in PNCM in lowlands at elevations from 128 to 280 m. *Pteropsiella metzgeriiformes* was collected at an elevation of 277 m, similar to Pinzón (2003), who reported this species between 100 and 300 m. According to Gradstein (1995), the diversity of thalloid liverworts species is highest on plains (83 species) with an elevation range of 0–1200 m. One possible reason for this is that Marchantiales are drought-resistant plants which do not need permanent humidity and require open places with full-sun exposure (Bischler-Causse et al. 2005). According to Gradstein and Costa (2003), several species of liverworts are found in Brazil at elevations of 0–200 meters, which reflects the large latitudinal extension of the country's humid plains. Some thalloid liverwort species were found to be restricted to certain localities and habitats in PNCM; for example, *Cronisia weddellii*, *Riccia vitalii*, and *R. stenophylla* were only found near waterfalls and along the banks of the Rio Farinha, usually on rocks or in places partially exposed to the sun.

We found the diversity of thalloid liverwort species in PNCM to be 16% of the species known from northeastern Brazil. In comparison to other studies on thalloid liverworts in the Brazilian Cerrado, we did not find four families, Marchantiaceae, Dumortieraceae, Metzgeriaceae, and Pelliaceae, in PNCM. We believe that these families may occur in Maranhão and in PNCM, as there are still areas in the state and park that are still unexplored. More fieldwork is needed to better understand the diversity of thallose liverworts, as well as other bryophytes, in this state and national park. Our search for thalloid liverwort specimens on the SpeciesLink website (SpeciesLink 2020) yielded only nine records for all herbaria, revealing a scarcity of collections of these plants from Maranhão and demonstrating the need for more collections and increased study of thalloid liverworts.

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Authors' Contributions

JASS and FPO collected the plants; JASS photographed the plants; JASS, RSF and DPC identified the plants; FPO and RSF edited the images and financed the collecting expeditions; JASS revised herbarium collections; JASS, FPO, DPC, and RSF wrote and revised the manuscript.

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